Hydrobiologia (2020) 847:2863–2872
https://doi.org/10.1007/s10750-020-04278-y

PRIMARY RESEARCH PAPER

Morphological differentiation in the widespread fish *Galaxias maculatus*: do darker environments imply bigger eyes?

Javier Hernán Rojo · Patricia Rodríguez · Claudia Clementina Boy

Received: 8 March 2019 / Revised: 18 February 2020 / Accepted: 27 April 2020 / Published online: 8 May 2020

Abstract The visual capacity of aquatic organisms is, in general, related to light penetration in the water. Therefore, aquatic environments that differ in color can potentially contribute to species polymorphism, especially in fish. In this study, we explore the relationship between light quality and intensity in water bodies and the eye and mouth size in *Galaxias maculatus*, one of the most widespread fish. Fish morphology was studied photographically, and the vertical attenuation coefficient of light (K_d) was measured in five aquatic systems: two humic lakes, two estuaries, and one river. Water color was also estimated as absorbance at 440 nm. In those environments with less light penetration and darker water color, we observed bigger eyes and, additionally, larger mouths. The darkness of water bodies was mainly related to water color associated with humic substances. As *G. maculatus* is known to be a visual predator, our results suggest that bigger eyes increase visual capacity in darker environments, which would result in improved feeding rates, also supported by larger mouth length.

Keywords Eye size · Mouth length · Galaxiidae · Light attenuation · Tierra del Fuego

Introduction

Compared to land, the visibility in water bodies is generally poorer and variable, predominantly due to attenuation and scattering caused by the substances present in the water and the light loss with depth (Utne, 1997). Light absorption in the aquatic media is attributed to four components: water itself, dissolved yellow substances, photosynthetic biota, and particulate matter (Kirk, 2011). The vertical attenuation coefficient (K_d) is a variable which integrates the absorption of all those components (Kirk, 2011). These factors influence how light penetrates the water and, consequently, how it affects the visual abilities of organisms. Dissolved yellow substances are included in the dissolved organic matter (DOM) or dissolved organic carbon (DOC) complex. DOC in most aquatic ecosystems is composed of up to 50% humic substances (Suhett et al., 2007) and is known to affect light attenuation in water (Curtis & Adams, 1995). DOC can modify the aquatic trophic structure through

---

Handling editor: David J. Hoeinghaus

J. H. Rojo (✉) · P. Rodríguez · C. C. Boy
Centro Austral de Investigaciones Científicas (CADIC) – CONICET, Bernardo Houssay 200 (V9410BFD), Ushuaia, Argentina
e-mail: javierhrojo@gmail.com

P. Rodríguez
Instituto de Ciencias Polares, Ambiente y Recursos Naturales (ICPA), Universidad Nacional de Tierra del Fuego, Ushuaia, Argentina

decreasing primary production by reducing the light that reaches the autotrophs and by acting as a source of energy for bacteria (Jones, 1992). Additionally, humic substances often affect water color, which can be estimated with the water absorbance at 440 nm (g_{440}) in most inland and estuarine waters (Kirk, 2011).

Different life strategies in a given species can favor polymorphism as a result of different evolutionary forces such as genetic drift, migration, or adaptation to different environments. This is especially prevalent in fish, as they are more susceptible than other vertebrates to morphological variation induced by environmental factors (Ferriz & Gómez, 2015). A decrease in water transparency is known to affect; visual feeding (e.g., Vinyard & O'Brien, 1976), predators avoidance (e.g., Ljunggren & Sandström, 2007) and communication (e.g., Maan et al., 2010). Different environments drive adaptations that increase fitness, eventually leading to speciation (McPhail, 1984). The eyes of mammals, birds, amphibians, reptiles, and some elasmobranchs have muscle mechanisms to control the amount of light they detect (Douglas et al., 1998). However, most teleost cannot increase or reduce the pupil's size because their iris is immobile (Helfman et al., 2009). Thus, the amount of light they detect (i.e., photons) depends on the conditions of the luminosity of the environment which is affected by factors such as depth, water color, or turbidity.

Like any other sensorial system, vision requires high energy expenditure (Niven & Laughlin, 2008). Hence, from an evolutionary point of view, in environments where light penetration is low, there is a trade-off between developing larger eyes or losing them completely (Dugas & Franssen, 2012). Energy acquisition is intrinsically related to feeding (Moran et al., 2015). The development of efficient visual structures contributes to the improvement of efficient feeding systems, such as a larger mouth, or changes in foraging behavior, since larger prey may be more visible (Carter et al., 2010). More so, according to the optimal foraging theory, individuals with a larger mouth can maximize energy allocation by feeding on larger prey items, resulting in increased fitness. Fish can detect their predators through visual, acoustic, or chemical signals (Milano et al., 2010). For an object to be visible, whether prey or a predator, a physiological threshold (ability to detect light) of contrast with the surroundings must be overcome (Aksnes & Giske, 1993). In the case of fish, the threshold depends on factors such as the size of the object and the intensity of the light (Anthony, 1981). For this reason, fish feeding efficiency and capacity to detect predators may decrease with higher turbidity or darker water color (Hecht & van der Lingen, 1992).

Galaxias maculatus (Jenyns, 1842) is one of the world's most widespread fish and is native to the Southern hemisphere (McDowall, 1968). It has two life strategies: diadromous (amphidromous), where its larval stage develops in the sea; and landlocked, where its entire life cycle develops in lakes, lagoons, or rivers (e.g., Cussac et al., 1992). It is considered a carnivorous species that is a visual predator, mostly on macroinvertebrates (McDowall, 1968). Across its wide geographical range, the species exhibits a great plasticity in its life history including diadromous and landlocked populations, reproduction, maximum size of individuals, morphological variation and behavior (McDowall, 2003; Chapman et al., 2006; Boy et al., 2009; Barbee et al., 2011; Barriga et al., 2012; Rojo et al., 2018). It has previously been described that its foraging efficiency decreases with increasing turbidity (Rowe & Dean, 1998) and that its vision is not only crucial for feeding but also to avoid predators (Milano et al., 2010).

The aim of this work is to investigate phenotypic differences in eye and mouth size of *G. maculatus* in five water bodies of Tierra del Fuego with distinct light climates: two brown humic lakes and three clear water bodies (two estuaries and one river).

Materials and methods

Sampling individuals

Sampling was performed between January 2015 and January 2019 in two estuaries, Arroyo Negro (AN, 54° 50′ 53″ S, 68° 34′ 51″ W) and Bahía Varela (BV, 54° 52′ 22″ S, 67° 16′ 29″ W); two humic lakes, Laguna Cecilia (LC, 54° 49′ 52″ S, 68° 34′ 37″ W) and Laguna Negra (LN, 54° 50′ 45″ S, 68° 35′ 31″ W); and one river, Río Grande (RG, 53° 49′ 16″ S, 67° 52′ 58″ W) (Fig. 1).

Galaxias maculatus were collected with a trawl net (10 m long, 1 m high, 5 mm mesh size) two hours after high tide in AN ($n = 60$) and BV ($n = 40$), and with an electrofishing equipment (Smith-Root, Inc. model LR-24, Vancouver, WA, USA) with 400 V, frequency of

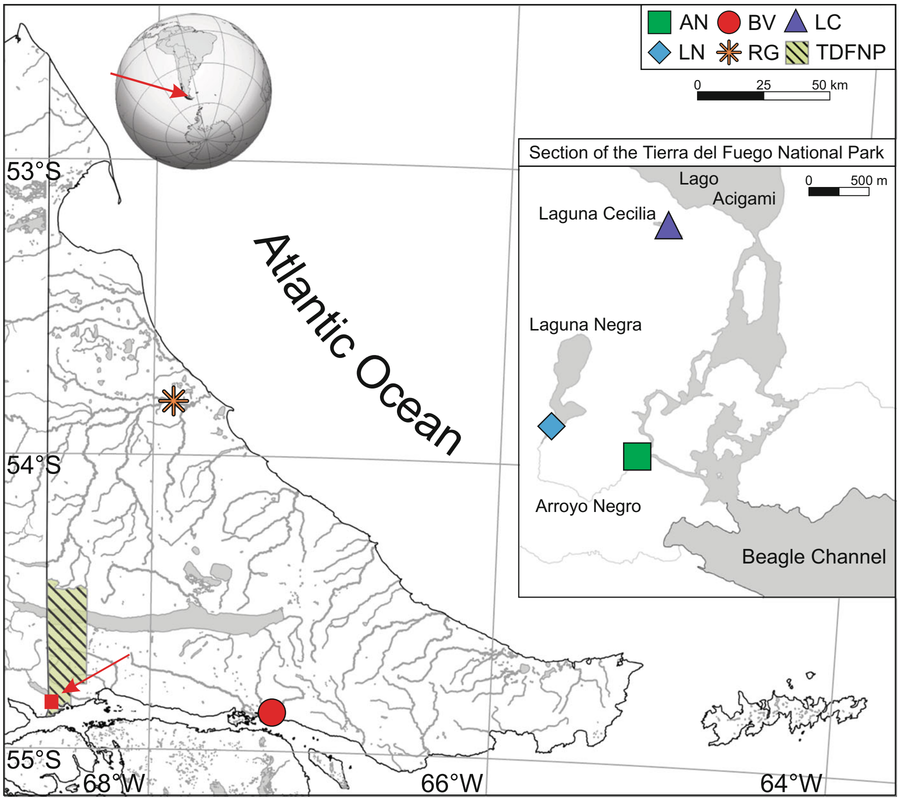

Fig. 1 Sampling sites of *Galaxias maculatus* in Tierra del Fuego. *AN* Arroyo Negro, *BV* Bahía Varela, *LC* Laguna Cecilia, *LN* Laguna Negra, *RG* Río Grande, *TDFNP* Tierra del Fuego National Park. Inset: section of the TDFNP showing sampling sites

100 Hz and duty cycle of 2 ms in LC ($n = 40$), LN ($n = 60$) and RG ($n = 45$), counting a total of 245 individuals. Fish were taken to the laboratory in aerated 100 l tanks with water at environmental temperature. In the laboratory, fish were euthanized with tricaine methanesulfonate (MS-222, Sigma-Aldrich, St. Louis, MO, USA) in a concentration above 300 mg of MS-222 per liter of water.

Environmental parameters

Dissolved oxygen, conductivity, pH, and water temperature were measured in each water body with a Hanna HI9828 multiparameter probe (Hanna Instruments, Inc., Woonsocket, RI, USA). Photosynthetic active radiation (PAR) was measured every five centimeters in the water column with a light meter Li-250A equipped with a spherical quantum sensor Li-193SA (Li-Cor, Lincoln, NE, USA). The vertical attenuation coefficient, K_d (in m^{-1}; $n = 3, 1, 2, 3$ and 2 for AN, BV, LC, LN and RG, respectively), was obtained as the slope of the linear regression of the natural logarithm of PAR versus depth (Kirk, 2011).

Water samples (2 in AN, 1 in BV, 2 in LC, 3 in LN and 1 in RG) were taken from each water body for further measurements of absorbance at 440 nm in a GBC Cintra 10e spectrophotometer (GBC Scientific, Braeside, Australia) in water filtered through Whatman GF/F filters. The absorption coefficient at 440 nm is used here as a water color proxy (g_{440}, Kirk, 2011). Suspended solids concentration (SS) was obtained by filtering a known volume of water through pre-dried and weighed MG-C filters of 1.2 µm pore size. The filters with the solids were dried (60°C) until constant weight and weighed again (APHA, 2005).

Eye size and mouth length

Total length (TL) and standard length (SL) of all individuals were measured with an accuracy of 0.01 mm. After the individuals were euthanized, photographs of the left side of each individual were taken with a 16-megapixel digital camera mounted on a photographic stand with a scale reference. The following five homologous points (landmarks) were digitized with the software tpsDig2 v2.22 (Rohlf, 2015): 1. The anterior end of the premaxilla, 2. Posterior end of the mouth corner, 3. The anterior end of the eye, 4. Eye center, 5. Posterior end of the eye (Fig. 2).

The diameter of the eye (ED) and the mouth length (ML) were measured as the Euclidean distance between landmarks 3 and 5 for ED and between 1 and 2 for ML, and their relationships with the standard length (EDR and MLR, respectively) was calculated by $\mathrm{EDR} = \frac{\mathrm{ED}}{\mathrm{SL}} \times 100$ and $\mathrm{MLR} = \frac{\mathrm{ML}}{\mathrm{SL}} \times 100$.

Statistical analyses

All statistical analyses were performed using R (R Core Team, 2018). The comparisons of EDR and MLR among sampling sites were analyzed using a Dunn test after the Kruskal–Wallis test with the *dunn.test* package (Dinno, 2017), since the assumptions of normality and homoscedasticity were not met, and transformations did not improve the fit.

In addition, Pearson correlations were made between K_d and water temperature and g_{440}. Spearman correlations were made between K_d and EDR and MLR; g_{440} and EDR and MLR; and between SS and EDR and MLR since the assumption of normality for EDR and MLR was not met.

Results

Dissolved oxygen was similar among sites, ranging between 9.1 and 12.3 ppm. Conductivity was higher in Arroyo Negro, probably due to the influence of the tide during sampling provided its proximity to Beagle Channel (Fig. 1). The pH was also similar among sites, ranging between 6.9 and 8.2 (Table 1). During the study, the K_d ranged between 0.43 and 2.4 m^{-1} for Arroyo Negro in January and Laguna Cecilia in April, respectively. The absorbance at 440 nm (g_{440}) ranged between 0.07 and 2.52 m^{-1} for Arroyo Negro in January and Laguna Cecilia in February, respectively. Suspended solids concentration (SS) ranged between 0.44 $\mathrm{mg\ l}^{-1}$ in Laguna Negra and 7.05 $\mathrm{mg\ l}^{-1}$ in Bahía Varela (Table 1).

The K_d was not dependent on water temperature as revealed by the lack of significant correlation between K_d and water temperature ($n = 9$; $r = 0.30$; $P = 0.43$). Hence, we dismiss seasonal effects in the interpretation of our results. K_d and g_{440} were positively correlated ($n = 9$, $r = 0.77$, $P < 0.05$).

Total length of *G. maculatus* individuals ranged between 41.7 and 103.4 mm. Relative eye diameter (EDR) ranged between 3.74 for Bahía Varela and 6.16 for Laguna Negra (Table 1). Relative mouth length (MLR) ranged between 3.85 for Arroyo Negro and 7.37 for Laguna Negra. EDR and MLR were significantly different among sampling sites (Kruskal–Wallis, $X^2 = 179.27$, $P < 0.05$; $X^2 = 118.48$, $P < 0.05$, respectively) (Fig. 3). Both EDR and MLR were significantly larger in humic lakes (Laguna Cecilia and Laguna Negra) than in the rest of the sites, with clearer waters (Arroyo Negro, Bahía Varela and Río Grande)

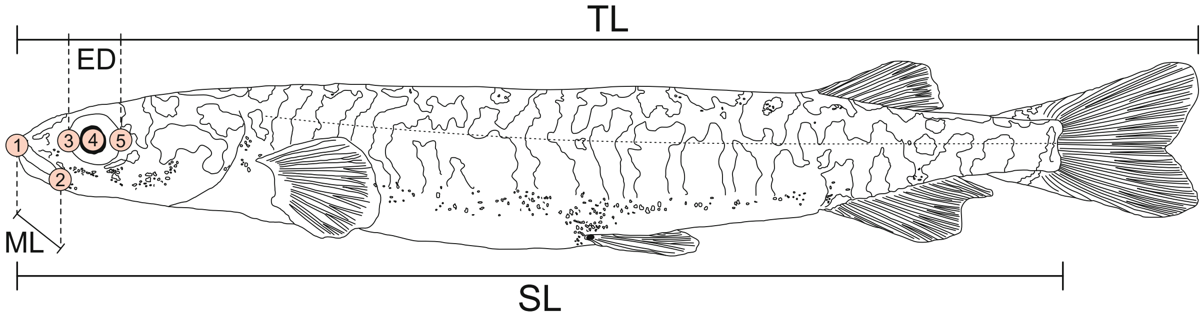

Fig. 2 Morphological measurements and location of the landmarks used in the morphometry analysis of *Galaxias maculatus* from the five sampling sites in Tierra del Fuego. **1**. The anterior end of the premaxilla, **2**. Posterior end of the mouth corner, **3**. The anterior end of the eye, **4**. Eye center, **5**. Posterior end of the eye. Total length (TL), standard length (SL), eye diameter (ED), mouth length (ML)

Table 1 Morphometric variables from *Galaxias maculatus* and environmental parameters from the sampling sites in Tierra del Fuego

Site	DO (ppm)	C (µS cm^{-1})	pH	K_d (m^{-1})	g_{440} (m^{-1})	SS (mg l^{-1})	EDR	MLR
AN	10.61	188–4918	6.99–7.54	0.75 (0.43–0.91)	0.51 (0.07–0.96)	1.05–1.57	4.63 ± 0.33^{ac}	5.26 ± 0.63^{a}
BV	9.62	39–140	7.46–8.22	0.46	nd	7.05	4.31 ± 0.36^{a}	5.21 ± 0.44^{a}
LC	9.8–11.1	93–105	6.99–7.41	2.3 (2.2–2.4)	2.46 (2.41–2.52)	1.5–2.35	5.72 ± 0.25^{b}	6.67 ± 0.38^{b}
LN	9.1–12.3	58–99	6.89–8.2	1.29 (1–1.76)	0.94 (0.58–1.51)	0.44–1.47	5.65 ± 0.27^{b}	6.07 ± 0.58^{c}
RG	10.5	71–101	7.12–8.11	1.35 (1.08–1.63)	0.18	3.65	4.77 ± 0.36^{c}	5.47 ± 0.59^{a}

AN Arroyo Negro, *BV* Bahía Varela, *LC* Laguna Cecilia, *LN* Laguna Negra, *RG* Río Grande, *DO* dissolved oxygen, *C* conductivity, K_d vertical attenuation coefficient, g_{440} absorption coefficient at 440 nm, *SS* suspended solids, *EDR* relative eye diameter, *MLR* relative mouth length

For DO, C, pH, and SS, the range is shown when available. For K_d and g_{440}, the mean and the range (in parentheses), when available, are shown. For EDR and MLR, the mean ± standard deviation are shown. *nd* non detectable. Different lowercase letters denote significant differences between sampling sites (Dunn test, $\alpha = 0.05$)

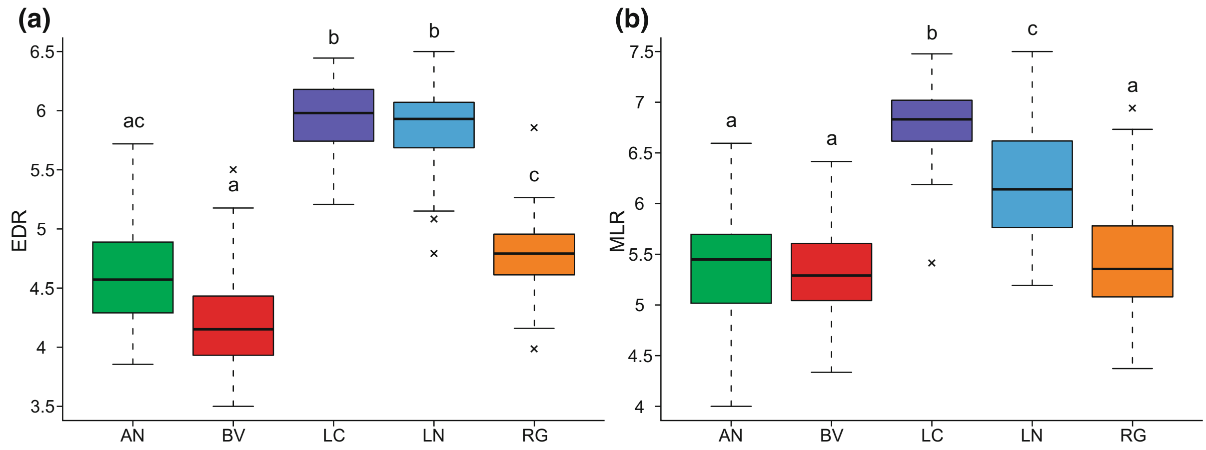

Fig. 3 **a** Relative eye diameter (EDR) and **b** relative mouth length (MLR) of *Galaxias maculatus* from sampling sites in Tierra del Fuego. *AN* Arroyo Negro, *BV* Bahía Varela, *LC* Laguna Cecilia, *LN* Laguna Negra, *RG* Río Grande. Thin lines represent maximum and minimum values, the bottom and the top of the box represent the 25% and 75% quartile, respectively, the bold line indicates the median and the × indicate outliers. Different lowercase letters denote significant differences between sampling sites (Dunn test, $\alpha = 0.05$)

($X^2 = 166.21$, $P < 0.05$ and $X^2 = 102.97$, $P < 0.05$, respectively), being EDR 20% and MLR 17% higher in humic lakes.

Both the EDR and MLR were positively correlated with the K_d ($n = 11$, $r_s = 0.87$, $P < 0.05$ and $r_s = 0.84$, $P < 0.05$, respectively) and with g_{440} ($n = 9$, $r_s = 0.76$, $P < 0.05$ and $r_s = 0.83$, $P < 0.05$, respectively); but not with SS ($n = 9$, $r_s = -0.34$, $P = 0.38$ and $r_s = -0.20$, $P = 0.61$, for EDR and MLR, respectively) (Fig. 4). In addition, EDR and MLR were positively correlated ($n = 11$, $r_s = 0.72$, $P < 0.05$).

Discussion

In this study, we show that the eye size of *G. maculatus*, a possible *proxy* for its visual capacity, is larger in fish inhabiting environments with poor light penetration than in clear water environments. Water transparency, either due to turbidity or color, affects several processes in aquatic ecosystems, such as intraspecific behavior and interactions in the case of fish that depend on their visual capacity (e.g., Heubel & Schlupp, 2006; Ljunggren & Sandström, 2007). Turbidity and color affect water transparency

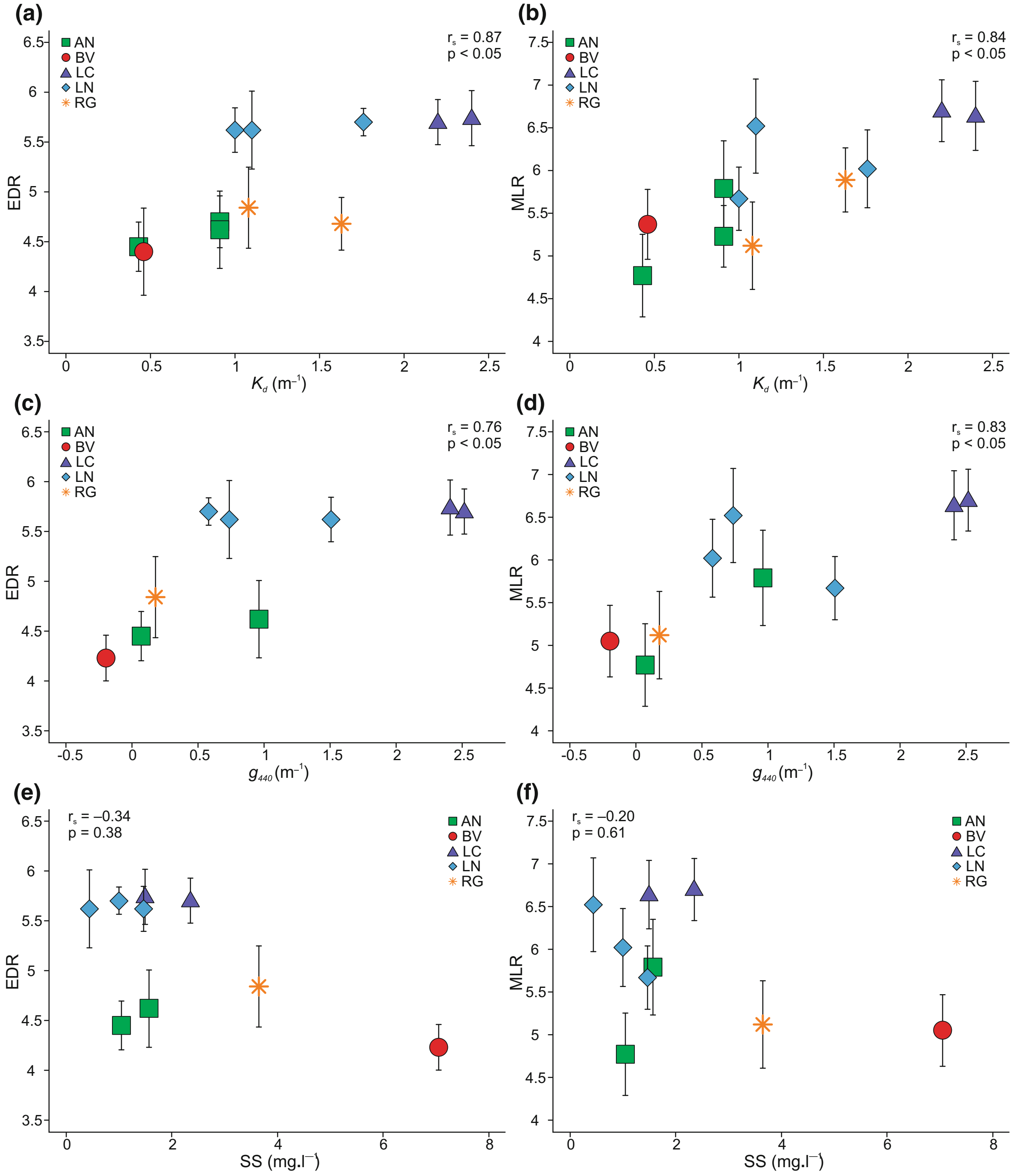

Fig. 4 Morphometric variables in relation to environmental variables for *Galaxias maculatus* of the five sampling sites in Tierra del Fuego. **a** Relative eye diameter (EDR) and the light attenuation coefficient (K_d), **b** relative mouth length (MLR) and K_d, **c** EDR and the absorption coefficient at 440 nm (g_{440}), **d** MLR and g_{440}, **e** EDR and suspended solids concentration (SS) and **f** MLR and SS. *AN* Arroyo Negro, *BV* Bahía Varela, *LC* Laguna Cecilia, *LN* Laguna Negra, *RG* Río Grande. For EDR and MLR, the mean ± standard deviation is shown

independently (Koenings & Edmundson, 1991) and have different effects on fish survival and feed efficiency. For example, the exogenous feeding of walleye fry [*Sander vitreus* (Mitchill, 1818)] starts earlier in turbid water than in dye-colored water (Bristow et al., 1996). Due to variations in water transparency, organisms can change their feeding strategy or exploitation of food resources, for instance, from small to larger prey, and this can affect their morphology (e.g., Breck, 1993; Magnhagen & Heibo, 2001). *G. maculatus* is described as a visual predator (McDowall, 1968) and has larger eyes than other species of *Galaxias* (McDowall, 1990; Rowe & Dean, 1998). Therefore, its foraging ability is expected to have a close relationship with visibility, since larger eyes often have better resolution (Li et al., 1985). It is also expected that foraging ability is related to reactive distance imposed by the different environments, i.e., the largest distance at which a fish can locate prey or predator (Vinyard & O'Brien, 1976). Hence, Rowe & Dean (1998) found in culture ponds that as turbidity increased, juvenile *G. maculatus* decreased their feeding ability. Consequently, the larger eye diameter found in Laguna Cecilia and Laguna Negra individuals (20% greater than in Arroyo Negro, Bahía Varela, and Río Grande individuals) could be an adaptation to the reduction of the penetration of light. Similar results were reported by Bartels et al. (2016) which found larger eye size with increasing DOC concentrations (i.e., high concentration of humic substances) in perch (*Perca fluviatilis,* Linnaeus, 1758). Dugas & Franssen (2012) observed in the cyprinid *Cyprinella lutrensis* (Baird & Girard, 1853) a positive association between eye size and turbidity (i.e., larger eye size in turbid environments). Lattuca et al. (2007) also found a relationship between lower water transparency of Andean-Patagonian lakes and a larger eye size in juveniles of *Aplochiton zebra* Jenyns, 1842. In regard to the retina of *G. maculatus*, Ali et al. (1990) found differences between individuals from light and 'dark' running waters, mainly in the location of the cones, although no light measurements from the environment were reported. Thus, individuals of *G. maculatus* from different light climates would not only present differences in the structure of the retina as suggested by Ali et al. (1990), but also, as our study suggest, in the eye size.

In the studied lakes (Negra and Cecilia), low light penetration is mainly related to the color of the water due to the high amounts of colored dissolved organic carbon (DOC, ca. 8 and 16 mg l^{-1} in Laguna Negra and Laguna Cecilia, respectively; Rodríguez unpublished) and not due to turbidity or suspended solids concentration. In addition, the positive relationship between K_d and the absorbance at 440 nm shows that humic substances have a direct and positive effect on total K_d (i.e., the higher g_{440}, the higher total K_d) since the total K_d depends on the light absorption of water itself, phytoplankton, tripton and humic substances (i.e., $K_d = K_{dW} + K_{dPhi} + K_{dTri} + K_{dG}$). For instance, in Laguna Negra, both turbidity and suspended solids concentrations are in general low (ca. 1.5 NTU and about 0.9 mg l^{-1}, respectively, data not shown). Thus, turbidity (i.e., dissolved or suspended substances which scatter light) might not determine the light environment in these humic lakes. Even though turbidity could not be measured in Laguna Cecilia, it can be suggested that its values are similar to Laguna Negra since suspended solids concentration was also low, and color, and K_d were also high. In these humic lakes, the larger contribution to the water color is probably because the southern lakes of the Isla Grande de Tierra del Fuego usually contain high amounts of humic substances due to the large biomass of *Sphagnum* sp., which give them their characteristic brown color (Saad et al., 2016). Although in this study, we observed that the smaller the light penetration, the greater the eye size, preliminary results suggest that the DOC threshold of the visual capacity of *G. maculatus* should be lower than 50 mg l^{-1}. In a highly humic lake from the east of Tierra del Fuego (54° 58′ 1.41″ S, 66° 43′ 54.33″ W) with severe light limitation due to high concentrations of humic substances ($K_d = 6$ m^{-1}; ca. 50 mg l^{-1} in DOC, Rodríguez unpublished), no fish were captured. However, as pH in the mentioned lake is around 4, more research is needed to test whether light or light plus another environmental factor besides fish distribution is limiting *G. maculatus* in highly humic lakes from the east of the island.

In addition, the mouth length was larger in the environments with less light penetration. This could be an adaptation related to the size of the prey and feeding efficiency (e.g., Karpouzi & Stergiou, 2003). Larger mouth length in darker environments would increase feeding efficiency, increasing the capacity of individuals to ingest larger prey, that we presume more detectable than smaller ones in such environments.

Vinyard & O'Brien (1976) working with a turbidity gradient of clay sediments in the bluegill *Lepomis macrochirus* Rafinesque, 1819, found at low turbidity conditions (6.25 or 10 Jackson Turbidity Units, JTU) a positive linear relationship between reactive distance and prey size, which diminished in high turbidity conditions (30 JTU), where reactive distance was independent of the prey size. However, we cannot expect the same response as turbidity in our dark sites was low. Mouth length, among other morphological characteristics (e.g., fins shape and location, body depth, coloration), in many cases, influence the niche occupied by organisms (Karpouzi & Stergiou, 2003). Our results regarding mouth length —larger in Laguna Cecilia individuals, intermediate in individuals from Laguna Negra and smaller in Arroyo Negro, Bahía Varela, and Río Grande—could be related to feeding ecology and behavior, as has been described in other species (e.g., Keast & Webb, 1966; Norton, 1991). For instance, in *A. zebra*, a relationship has been found between the shape of the mouth and the gape size with the geographic distribution in different lakes and diet (Lattuca et al., 2007). According to the optimal foraging theory, those individuals who feed more efficiently (i.e., ingesting larger prey) and maximize their energy allocation, have greater fitness and thus contribute more to offspring (e.g., Pyke, 1984; Tytler & Calow, 1985).

We observed a similar eye and mouth length in Arroyo Negro, Bahía Varela, and Río Grande. These sites present different limnological conditions but similar light climates, which widen the extent of our results. For example, as Arroyo Negro and Bahía Varela are estuaries, differences in tide influence or current velocity can be found between these two clear water systems and Río Grande, which is a clear water river. These differences did not hinder us from detecting a clear pattern of smaller eyes with clear waters. This strengthens the hypothesis that the water color could be one of the strongest modeling factors in the environment regarding eye size and mouth length of *G. maculatus*.

We conclude that individuals of *G. maculatus* that inhabit environments with less light penetration have larger eyes, probably related to improved feeding efficiency and predator avoidance. We also observed individuals with larger mouths in darker environments, which we discuss as an advantage to catch larger prey. Our results also indicate that color, due to higher concentrations of humic substances, was the driving force influencing light attenuation in these environments. Furthermore, the largest relative eye diameter was observed in more isolated populations, potentially related to a lesser gene flow and genetic drift in the landlocked populations (Laguna Cecilia and Laguna Negra) than in the diadromous ones (Arroyo Negro, Bahía Varela, and Río Grande), due to less migration or smaller population size. The results found could be strengthened through experimental laboratory corroboration to evaluate the larger eye-better vision assumption. For example, by measuring the reaction time of adult individuals with different eye size, or by measuring the eyes diameter in individuals reared at different light conditions. In addition, further studies of the retina, as well as diet and food availability, are needed in these populations of *G. maculatus* to fill the gaps in the knowledge of the species. Also, the relationship between morphology and population genetic structure is worth to study in search of a better comprehension of the wide polymorphism of *G. maculatus*' populations.

Acknowledgements The authors thank Sonia Rimbau, Daniel Aureliano, Maximiliano Rubel, Victoria García, and Florencia Veira for their collaboration in the field and the laboratory. Especially thanks are due to Dr. Pia Bartels for the critical read and language edition on this manuscript. This research was supported by CONICET (PIP 0440, P-UE 2016), Agencia Nacional de Promoción Científica y Tecnológica (PICT 2014-1804, PICT 2015-1152), Administración de Parques Nacionales (Projects 1038 and 032CPA).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All sampling procedures and experimental manipulations follow the guidelines approved by the Universidad de Buenos Aires from Argentina (Facultad de Ciencias Exactas y Naturales, Bioterio Central, https://exactas.uba.ar/cicual/).

References

Aksnes, D. L. & J. Giske, 1993. A theoretical model of aquatic visual feeding. Ecological Modelling 67: 233–250.

Ali, M., S. Sakurai & S. P. Collin, 1990. Adaptative radiation of the retina in Galaxiidae (Salmoniformes). Australian Journal of Zoology 38(2): 173–186.

Anthony, P. D., 1981. Visual contrast thresholds in the cod *Gadus morhua*. Journal of Fish Biology 19: 87–103.

APHA, 2005. Standard Methods for the Examination of Water and Wastewater, 21st ed. American Public Health Association, Washington, DC.

Barbee, N. C., R. Hale, J. Morrongiello, A. Hicks, D. Semmens, B. J. Downes & S. E. Swearer, 2011. Large-scale variation in life history traits of the widespread diadromous fish, *Galaxias maculatus*, reflects geographic differences in local environmental conditions. Marine and Freshwater Research 62: 790–800.

Barriga, J. P., M. Á. Battini, M. García-Asorey, C. Carrea, P. J. Macchi & V. E. Cussac, 2012. Intraspecific variation in diet, growth, and morphology of landlocked *Galaxias maculatus* during its larval period: the role of food availability and predation risk. Hydrobiologia 679: 27–41.

Bartels, P., P. E. Hirsch, R. Svanbäck & P. Eklöv, 2016. Dissolved organic carbon reduces habitat coupling by top predators in lake ecosystems. Ecosystems 19(6): 955–967.

Boy, C. C., A. F. Pérez, M. E. Lattuca, J. Calvo & E. Morriconi, 2009. Reproductive biology of *Galaxias maculatus* (Jenyns 1842) in Río Ovando estuary, a high-latitude environment in southernmost Patagonia. Journal of Applied Ichthyology 25: 661–668.

Breck, J. E., 1993. Foraging theory and piscivorous fish: are forage fish just big zooplankton? Transactions of the American Fisheries Society 122(5): 902–911.

Bristow, B. T., R. C. Summerfelt & R. D. Clayton, 1996. Comparative performance of intensively cultured larval walleye in clear, turbid, and colored water. The Progressive Fish-Culturist 58(1): 1–10.

Carter, M. W., D. E. Shoup, J. M. Dettmers & D. H. Wahl, 2010. Effects of turbidity and cover on prey selectivity of adult smallmouth bass. Transactions of the American Fisheries Society 139(2): 353–361.

Chapman, A., D. L. Morgan, S. J. Beatty & H. S. Gill, 2006. Variation in life history of land-locked lacustrine and riverine populations of *Galaxias maculatus* (Jenyns 1842) in Western Australia. Environmental Biology of Fishes 77: 21–37.

Curtis, P. J. & H. E. Adams, 1995. Dissolved organic matter quantity and quality from freshwater and saltwater lakes in east-central Alberta. Biogeochemistry 30: 59–76.

Cussac, V. E., P. M. Cervellini & M. A. Battini, 1992. Intralacustrine movements of *Galaxias maculatus* (Galaxiidae) and *Odontesthes microlepidotus* (Atherinidae) during their early life history. Environmental Biology of Fishes 35: 141–148.

Dinno, A., 2017. Dunn's Test of Multiple Comparisons Using Rank Sums. R package version 1.3.5. https://CRAN.R-project.org/package=dunn.test. Accessed 7 May 2020.

Douglas, R. H., R. D. Harper & J. F. Case, 1998. The pupil response of a teleost fish, *Porichthys notatus*: description and comparison to other species. Vision Research 38: 2697–2710.

Dugas, M. B. & N. R. Franssen, 2012. Red shiners (*Cyprinella lutrensis*) have larger eyes in turbid habitats. Canadian Journal of Zoology 90: 1431–1436.

Ferriz, R. A. & S. E. Gómez, 2015. Polimorfismo en poblaciones diadrómicas y lacustrinas de *Galaxias maculatus*, Argentina, Sudamérica. Bioikos 29(2): 19–25.

Hecht, T. & C. D. van der Lingen, 1992. Turbidity-induced changes in feeding strategies of fish in estuaries. South African Journal Zoology 27(3): 95–107.

Helfman, G. S., B. B. Collette, D. E. Facey & B. W. Bowen, 2009. The Diversity of Fishes, 2nd ed. Wiley, Chichester.

Heubel, K. U. & I. Schlupp, 2006. Turbidity affects association behaviour in male *Poecilia latipinna*. Journal of Fish Biology 68(2): 555–568.

Jenyns, L., (1842). Part IV, Fish. In Darwin, C. (ed) The zoology of the voyage of HMS Beagle, under the command of Captain Fitzroy, RN during the years 1832 to 1836. London: Smith, Elder & Co.

Jones, R. I., 1992. The influence of humic substances on lacustrine planktonic food chains. Hydrobiologia 229: 73–91.

Karpouzi, V. S. & K. I. Stergiou, 2003. The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. Journal of Fish Biology 62: 1353–1365.

Keast, A. & D. Webb, 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. Journal Fish Research Board Canada 23(12): 1845–1874.

Kirk, J. T. O., 2011. Light and Photosynthesis in Aquatic Ecosystems, 3rd ed. University Press, Cambridge.

Koenings, J. P. & J. A. Edmundson, 1991. Secchi disk and photometer estimates of light regimes in Alaskan lakes: effects of yellow color and turbidity. Limnology and Oceanography 36(1): 91–105.

Lattuca, M. E., S. Ortubay, M. A. Battini, J. P. Barriga & V. E. Cussac, 2007. Presumptive environmental effects on body shape of *Aplochiton zebra* (Pisces, Galaxiidae) in northern Patagonian lakes. Journal of Applied Ichthyology 23: 25–33.

Li, K. T., J. K. Wetterer, J. Hairston & G. Nelson, 1985. Fish size, visual resolution, and prey selectivity. Ecology 66(6): 1729–1735.

Ljunggren, L. & A. Sandström, 2007. Influence of visual conditions on foraging and growth of juvenile fishes with dissimilar sensory physiology. Journal of Fish Biology 70(5): 1319–1334.

Maan, M. E., O. Seehausen & J. J. M. Van Alphen, 2010. Female mating preferences and male coloration covary with water transparency in a Lake Victoria cichlid fish. Biological Journal of the Linnean Society 99: 398–406.

Magnhagen, C. & E. Heibo, 2001. Gape size allometry in pike reflects variation between lakes in prey availability and relative body depth. Functional Ecology 15(6): 754–762.

McDowall, R. M., 1968. *Galaxias maculatus* (Jenyns), the New Zealand Whitebait. Fisheries Research Division, Marine Dept., Wellington.

McDowall, R. M., 1990. New Zealand Freshwater Fishes: A Guide and Natural History. Heinemann Reed, Auckland.

McDowall, R. M., 2003. Variation in vertebral number in galaxiid fishes (Teleostei: Galaxiidae): a legacy of life history, latitude and length. Environmental Biology of Fishes 66: 361–381.

McPhail, J. D., 1984. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*) – morphological and genetic evidence for a species pair in Enos Lake, British Columbia. Canadian Journal of Zoology 62: 1402–1408.

Milano, D., M. Lozada & H. E. Zagarese, 2010. Predator-induced reaction patterns of landlocked *Galaxias maculatus* to visual and chemical cues. Aquatic Ecology 44: 741–748.

Moran, D., R. Softley & E. J. Warrant, 2015. The energetic cost of vision and the evolution of eyeless Mexican cavefish. Science Advances 1(8): e1500363.

Niven, J. E. & S. B. Laughlin, 2008. Energy limitation as a selective pressure on the evolution of sensory systems. Journal of Experimental Biology 211: 1792–1804.

Norton, S. F., 1991. Capture success and diet of cottid fishes: the role of predator morphology and attack kinematics. Ecology 72(5): 1807–1819.

Pyke, G. H., 1984. Optimal foraging theory: a critical review. Annual Review of Ecology and Systematics 15: 523–575.

R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rohlf, J. F., 2015. tpsDig2, Digitize Landmarks and Outlines, 222nd ed. Department of Ecology and Evolution, State University of New York, Stony Brook.

Rojo, J. H., D. E. Figueroa & C. C. Boy, 2018. Age and growth of diadromous *Galaxias maculatus* (Jenyns 1842) in southernmost South America (54° S) including contribution of age classes to reproduction. Environmental Biology of Fishes 101(7): 1149–1160.

Rowe, D. K. & T. L. Dean, 1998. Effects of turbidity on the feeding ability of the juvenile migrant stage of six New Zealand freshwater fish species. New Zealand Journal of Marine and Freshwater Research 32(1): 21–29.

Saad, J. F., F. Unrein, P. M. Tribelli, N. López & I. Izaguirre, 2016. Influence of lake trophic conditions on the dominant mixotrophic algal assemblages. Journal of Plankton Research 38(4): 818–829.

Suhett, A. L., A. M. Amado, A. Enrich-Prast, F. D. A. Esteves & V. J. Farjalla, 2007. Seasonal changes of dissolved organic carbon photo-oxidation rates in a tropical humic lagoon: the role of rainfall as a major regulator. Canadian Journal of Fisheries and Aquatic Sciences 64: 1266–1272.

Tytler, P. & P. Calow, 1985. Fish Energetics: New Perspectives. Croom Helm, Sydney.

Utne, A. C. W., 1997. The effect of turbidity and illumination on the reaction distance and search time of the marine planktivore *Gobiusculus flavescens*. Journal of Fish Biology 50: 926–938.

Vinyard, G. L. & W. J. O'Brien, 1976. Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). Journal of the Fisheries Research Board of Canada 33(12): 2845–2849.